A Metapopulation Perspective on the Patch Dynamics of Giant Kelp in Southern California

Daniel C. Reed
Marine Science Institute, University of California, Santa Barbara, California, 93106 USA
Brian P. Kinlan
Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara California, 93106 USA
Peter T. Raimondi
Department of Ecology and Evolutionary Biology, University of California, Center for Ocean Health, Long Marine Lab, 100 Shaffer Road, Santa Cruz, California, 95060 USA
Libe Washburn
Institute for Computational Earth System Science, Department of Geography, University of California, Santa Barbara California, 93106 USA
Brian Gaylord
Marine Science Institute, University of California, Santa Barbara, California, 93106 USA
Patrick T. Drake
Department of Ecology and Evolutionary Biology, University of California, Earth and Marine Sciences Building, 1156 High Street, Santa Cruz, California 95064 USA

Abstract

The giant kelp, *Macrocystis* is the world's largest alga and a conspicuous inhabitant of shallow subtidal reefs in cool waters of the Pacific and Southern Oceans. It grows in discrete patches of varying size that fluctuate greatly in time and space in response to a complex of biotic and abiotic factors. Here we synthesize existing information relevant to the metapopulation ecology of this prominent seaweed, and present new analyses on spore dispersal and patch structure/dynamics to estimate the level of connectivity among local populations occurring along a continuous 500 km section of coast in southern California, USA. A 34-year time series of monthly aerial surveys showed that patches in this region underwent frequent extinctions and recolonizations that occurred over time scales ranging from several months to as much as 13 years. Extinction probabilities were negatively correlated with patch size, and positively correlated with degree of isolation. In contrast, recolonization probabilities were positively correlated with patch size and negatively correlated with isolation. The vast majority of patches remained extinct for less than two years before being recolonized. Empirical and modeled estimates of spore dispersal resembled a negative power function, with the bulk of spores landing near parent patches and the tails of dispersal extending from tens of meters to several kilometers depending on oceanographic currents and waves. Results of analyses overlaying modeled estimates of dispersal with inter-patch distances revealed that an average patch may be completely isolated or be connected to up to five neighboring patches, depending on the oceanographic setting and the size, fecundity, and spacing of patches. The results of

these analyses, when viewed in the context of previous studies and observations, indicate that the metapopulation concept is very applicable to giant kelp in southern California and should prove useful in explaining its population dynamics, genetic structure, and ability to recover rapidly from disturbance.

I. Introduction

Large brown algae in the Order Laminariales are conspicuous inhabitants of shallow subtidal reefs in cool seas worldwide. This diverse group of seaweeds, known as kelps, consists of 27 genera that vary tremendously in size, morphology, life span, and habitat (Kain 1979, Dayton 1985, Estes and Steinberg 1988). Species differ greatly even within genera, as evidenced in *Laminaria* whose congeners include annuals and long-lived perennials inhabiting areas ranging from the tropics to the High Arctic, and from the intertidal down to depths of 70 m (Kain 1979). Most kelps are short in stature and extend no more than a meter or two from the bottom. They commonly occur in aggregations called beds, which often form a dense subsurface canopy near the sea floor. Several species, however, grow very large (up to 45 m in length). These “giant kelps” contain gas-filled structures that allow them to produce a floating canopy that extends to the surface in water depths as great as 30 m. Beds of these giant kelps are frequently called kelp forests because their vertical structure and multiple vegetation layers resemble terrestrial forests (Darwin 1860, Foster and Schiel 1985). Kelps are very fast growing, and kelp beds are considered to be among the most productive ecosystems in the world, comparable, for example, to tropical rain forests (Mann 1973, 1982). The ecology of kelp stands and the diverse communities that they support has been summarized in several comprehensive reviews (e.g., North 1971, Dayton 1985, Schiel and Foster 1986, Mann 1982, Witman and Dayton 2001).

The demographics and population dynamics of kelps are as wide ranging as the diverse morphologies and growth habits that characterize the Order. In this chapter we limit our discussions to the giant kelp *Macrocystis* – an extensively studied, ecologically important genus that is widely distributed in cool seas of the northern and southern hemispheres (Womersley 1954). *Macrocystis* forms extensive forests off the coast of California and a considerable amount is known about their biology and ecology in this region (see reviews by North 1971, 1994, Foster and Schiel 1985, Murray and Bray 1993). Discontinuities in hard substrate in the nearshore cause *Macrocystis* to be distributed in discrete patches of varying size that expand and contract in response to biotic and abiotic changes in the environment. The dynamic and sometimes asynchronous behavior of these patches has long been recognized, yet metapopulation theory has rarely been invoked to explain them. This is due in part to an insufficient understanding of the limits of dispersal in kelps, the conditions that promote exchange among discrete kelp patches, and the frequencies at which these conditions occur.

In this chapter we examine the patch dynamics of *Macrocytis* in southern California from a metapopulation perspective. We begin by synthesizing existing and new information pertaining to the metapopulation structure and dynamics of *Macrocystis* in the Southern California Bight. Next we review the biological and physical factors that affect colonization, and we present new empirical and theoretical estimates of spore dispersal distance for varying oceanic conditions. This information is used to estimate levels of connectivity among discrete kelp patches for different current regimes. We define connectivity as demographic exchange between patches, which in the case of giant kelp occurs primarily via the passive transport of propagules. We intentionally do not discuss mechanisms responsible for the maintenance of extant populations (e.g., short distance dispersal that results in self replenishment). Instead we focus on empirical and theoretical estimates of local population extinction, local population establishment (i.e., colonization), and immigration, which are considered to be "in the hearth of metapopulation ecology" (Hanski 1999). We emphasize studies done in southern California, the system with which we are most familiar, and we draw heavily from our own research when addressing issues pertaining to dispersal and connectivity among local populations. We conclude with a discussion of the applicability of the metapopulation concept to giant kelp, and identify future research needed to improve characterization of metapopulation dynamics in kelps and other seaweeds.

II. Dynamics of giant kelp populations

Local populations of *Macrocystis* fluctuate greatly in time and space in response to a complex of predictable (seasonal) and unpredictable events. Increased water motion associated with winter storms and swell is a major source of plant mortality (Dayton and Tegner 1984, Ebeling et al. 1985, Seymour et al. 1989). The frequency and intensity of storm events varies unpredictably among years, causing erratic annual fluctuations in population size (Rosenthal et al. 1974, Foster 1982, Dayton et al. 1992). Likewise, differences in depth and wave exposure cause rates of storm-related mortality to vary substantially among sites (Dayton et al. 1984, Graham et al. 1997, Edwards 2001). Prolonged periods of warm, nutrient-depleted water such as those associated with El Niño

Southern Oscillation (ENSO) events can lead to local (Zimmerman and Robertson 1985, Reed et al 1996) and widespread (Dayton and Tegner 1989) kelp loss, and prevent subsequent recovery. Finally, intensive grazing (most notably by sea urchins) can eliminate entire beds (reviewed in Dayton 1985, Foster and Schiel 1985, Harrold and Pearse 1987). Conditions that promote or suppress outbreaks of sea urchin grazing are often localized in southern California, which causes asynchrony in the dynamics of local populations in this region (Ebeling et al. 1985, Harrold and Reed 1985, Reed et al. 2000).

Population growth in *Macrocystis* is solely dependent on sexual reproduction; fragmentation, clonal growth, and other forms of vegetative reproduction do not occur. Recruitment of new plants occurs when favorable conditions of light, nutrients, and primary space coincide with periods of abundant spore supply. These factors are most likely to co-occur in the winter and spring and depend on both chance events and the local density of adult plants (Deysher and Dean 1986, Reed 1990, Graham 2000). Like many terrestrial forests, giant kelp forests have a complex vertical structure composed of several canopy layers. Competition for sunlight and space among canopy members plays an important role in regulating the recruitment of new individuals (Pearse and Hines 1979, Reed and Foster 1984, Dayton et al 1984, Reed et al. 1997). Adult *Macrocystis* are the dominant competitors for light (Dayton et al. 1999) and provide the nearest source of spores for recruitment. Disturbances that alter the abundance of adult plants can interact with density-dependent processes to produce kelp forests with qualitatively different dynamics and size structures (Nisbet and Bence 1989, Burgman and Gerard 1990, Dean and et al. 1989, Tegner et al. 1997).

Discrete stands of giant kelp go extinct and reappear at irregular intervals. Large-scale phenomena such as El Niño events occur unpredictably in time and can produce widespread kelp loss. For example, large waves and adverse growing conditions associated with the strong El Niños of 1982-1983 and 1997-1998, eliminated *Macrocystis* from most areas of southern California and Baja California (Dayton and Tegner 1989, Edwards 2001). The additive effects of smaller-scale, but equally intense disturbances, such as those resulting from intensive sea urchin and amphipod grazing can cause giant kelp to display much higher rates of local extinction and recolonization at some sites (Ebeling et al. 1985, Tegner and Dayton 1987).

Predictions from theoretical models also suggest that local populations of *Macrocystis* have a relatively high probability of extinction. Burgman and Gerard (1990) examined persistence in *Macrocystis* using a stage-structured population model that incorporated environmental and demographic stochasticity. Their model predicted a 60% chance that the adult density of a local population will fall to zero during a 20-year period; the occurrence of an El Nñno event increased the likelihood of extinction probability to 80%.

To assess the regional-scale generality of the above-mentioned field observations and model predictions, we estimated rates of patch extinction and colonization from long-term aerial observations of giant kelp forests in southern California. Since 1958, ISP Alginates, Inc., a San Diego-based kelp harvesting company, has conducted aerial surveys of *Macrocystis* beds in southern California. During these surveys observers use canopy area and density to gauge the biomass of kelp harvestable from the surface (0 to ~1 m depth); visual estimates of biomass are then calibrated to actual harvested amounts.

After a 10-year period of ground-truthing, aerial biomass estimation methods were standardized in January 1968. Subsequent surveys were carried out, on an approximately monthly basis, by one of two trained observers (D. Glantz, personal communication). Survey data were interpolated onto a regular monthly grid (B. Kinlan, unpublished data). Here, we use surveys conducted between January 1968 and October 2002 (418 months) from an approximately 500 km stretch of coast between Pt. Arguello and the U.S.-Mexico border (Figure 1).

These surveys provide a long-term record of the presence or absence of giant kelp canopy in administrative kelp beds defined by the California Department of Fish and Game (~2-20 km in along-coast extent; Figure 1), with sufficient temporal resolution to identify administrative bed-wide extinction and recolonization events. However, greater spatial resolution is needed to identify discrete patches of habitat that can potentially be colonized by giant kelp (i.e.; firm substrates at appropriate depth; hereafter referred to simply as "patches") as required for an analysis of metapopulation dynamics. To identify discrete patches of giant kelp habitat, we used digital maps of giant kelp canopy occurrence derived from aerial infrared imagery (~3-5 m resolution). Comprehensive surveys of the area from Pt. Arguello to the U.S.-Mexico border were made in 1989, 1999 and 2002 (California Dept. of Fish and Game). At least two of these surveys (1989, 2002) captured giant kelp canopies at their annual peak, and all three surveys were conducted in years when giant kelp biomass was near its 20-year high across the region (B. Kinlan, unpublished data). We therefore used the combined giant kelp canopy area identified by these three maps to approximate the distribution of giant kelp patches in each of the California Department of Fish and Game administrative beds (Figure 1).

Patches were defined as discrete areas in which the composite *Macrocystis* canopy (i.e., that estimated by overlaying images of the three aerial infrared surveys) was either contiguous, or separated by gaps of less than 500 m. Comparison with other digital giant kelp canopy maps available for smaller portions of this region (spanning, in some cases, >30 y and 200 km of coast) suggest that the combination of the chosen three region wide surveys done in 1989, 1999, and 2002 captured > 95% of habitat patches (North et al. 1993; B. Kinlan, unpublished data).

To estimate rates of patch extinction and colonization, we considered each patch within a given California Department of Fish and Game administrative bed to be "occupied" for any month where ISP Alginates noted the presence of surface canopy kelp in that administrative bed. We considered patches to have gone "extinct" when no surface canopy was detected within the area of the administrative bed for six or more consecutive months. Under most conditions, sub-surface juvenile plants would grow to form a surface canopy in six months or less (Foster and Schiel 1985). Note that all patches within the confines of a given administrative kelp bed are considered occupied whenever the biomass estimate exceeds zero, and conversely all are considered extinct when no canopy is detected. Consequently, this method could over- or under-estimate actual rates of extinction and colonization depending on the degree to which patches within an administrative kelp bed fluctuate synchronously. However, because each administrative kelp bed contains only a small number of discrete patches (mean = 2.8, interquartile range = 1 to 4) and patch fluctuations are positively auto correlated at small spatial scales (i.e., 1-10 km; B. Kinlan, unpublished data) the resultant biases in extinction and colonization rates should be relatively small.

At a regional scale, occupancy of the giant kelp habitat mosaic is extremely dynamic (Figure 2). During the 34-year study period, the estimated fraction of patches occupied in southern California approached 100% in some months, but dipped to ~0% after a major El Nino event (1982-1984). In fact, for much of the time from 1982-1984, no surface canopy was detected in the aerial biomass surveys. We know from diver surveys that some scattered sub-surface juveniles were present during this period (e.g. Dayton and Tegner 1984, Dayton et al. 1999), but clearly they did not grow to form significant surface canopies within our six-month "window" for defining extinction. This highlights the fact that, under very stressful environmental conditions *Macrocystis* may experience suppressed recruitment and growth of juvenile stages that delays the formation of a surface canopy (Dean and Jacobsen 1984, 1986, Kinlan et al. 2003). Delayed growth of juveniles could, in certain cases, lead to recovery of local populations even in the absence of nearby spore sources (Ladah et al. 1999), in a manner similar to the "propagule rain" effect described by Gotelli (1991).

Extinction probabilities, defined here as the monthly probability of a patch going from occupied to extinct, ranged from 0.005 to 0.292 (mean ± SD = 0.057 ± 0.063; Figure 3a). Recolonization probabilities, defined as the monthly probability of a patch going from extinct to occupied, ranged from 0.023 to 0.200 (mean ± SD = 0.080 ± 0.040; Figure 3b). These monthly rates agree with models and observations that suggest kelp forest patches are highly dynamic at the scale of months to years (e.g., the 0.8 probability of extinction in a 20 year period cited above corresponds to a monthly rate of just 0.003). On average, extinction of a patch in our study region lasted from six months to four years (Figure 4a), and patches remained occupied for one to five years (Figure 4b). However, in certain cases extinctions lasted as little as a few months or as much as 13 years (Figure 4c) and patches of kelp persisted for several months to 15 years (Figure 4d).

Extinction and recolonization rates varied with patch size and patch isolation (Figure 5). We used the square root of patch area as a measure of size, and the average size of surrounding patches weighted by the inverse square of distance as a measure of isolation (Thomas and Hanski 1997). Patch isolation explained more variation in extinction (Figure 5b) and recolonization (Figure 5d) rates than patch size (Figure 5a,c), suggesting that immigration rates are dependent on distance and source population size. The lower extinction rates in highly connected (i.e., low isolation) patches indicates that rescue effects may play an important role in patch dynamics (Brown and Kodrik-Brown 1977, Hanski 1999). The lower colonization rates in highly isolated patches (Figure 5d) indicates that immigration rates may limit recolonization of isolated patches. The statistical significance of the relatively low correlations between patch size and extinction (Figure 5a) and recolonization (Figure 5c) was driven primarily by the two or three largest patches. Large kelp forests may have a low chance of stochastic extinction because of their large population size. Moreover, the greater amount of suitable habitat in large kelp forests may increase the likelihood that at least some portion of the patch is recolonized. Collectively, these results confirm impressions from smaller-scale studies that kelp forests are dynamic mosaics, characterized by frequent extinction and recolonization from nearby patches.

III. Factors affecting colonization

A. Life history constraints

Basic knowledge of the kelp life history is important for understanding the dynamics of local populations and the degree of connectivity among them. A characteristic feature of all kelps is that they undergo an alternation of generations between a macroscopic diploid sporophyte (a spore-producing plant) and a microscopic haploid gametophyte (a gamete-producing plant) (Fritch 1945). Meiosis occurs in the adult sporophyte to produce male and female zoospores that are the primary dispersive stage. Following a relatively short dispersal period (i.e., hours to days; Reed et al. 1992, Gaylord et al. 2002) zoospores (hereafter referred to as spores) settle to the bottom and germinate into sessile, free-living, microscopic gametophytes. In contrast to most marine organisms, fertilization in kelps occurs after dispersal when a pheromone released by the female gametophyte triggers the liberation of sperm from the male gametophyte and guides the sperm to the non-motile egg (Müller 1981). The distance over which the pheromone is effective in attracting sperm is believed to be less than 1 mm (Boland et al. 1983). Consequently, recruitment into the sporophyte generation is largely confined to areas of relatively dense spore settlement (e.g. > 1 mm^{-2}) where the probability of encounter between male and female gametes is sufficiently high to ensure fertilization (Reed 1990, Reed et al. 1991). Thus a major constraint limiting the distances over which kelps are able to colonize is the dilution of spores that accompanies their dispersal. This constraint on colonization distance decreases with increasing size of the source population (Anderson and North 1966, Reed et al. 1997). This is because an increase in the concentration of spores at the point of release generally results in a proportional increase in the concentration of spores at a given distance from that point.

Some variants of this life history involving the production of sporophytes without fertilization (i.e., apomixis) have been described from laboratory cultures for several species of kelp, including *Macrocystis* (reviewed by Lewis 1996). However, the development of kelp sporophytes from unfused gametes (i.e., parthenogenesis) or from gametophytes that do not produce gametes (i.e., apogamy) typically results in abnormalities, and there is little evidence that kelp sporophytes produced via apomixis are common in nature.

B. Modes of colonization

Local emigration and immigration of *Macrocystis* occurs in one of two ways: via dispersal of microscopic spores or via the transport of large sporophytes that become dislodged and set adrift (hereafter referred to as "drifters"). The tiny biflagellated spore (~ 6 μm in diameter) is the only motile stage in an otherwise sedentary life form (kelp sperm are also motile, but are believed to disperse no farther than a few millimeters, Müller 1981, Boland et al. 1983). Swimming speeds of kelp spores are relatively slow (~ 180 $\mu m\ s^{-1}$, C. Amsler personal communication), however, and the distances that spores disperse are determined largely by advective currents and vertical mixing (Gaylord et al. 2002). Factors that influence these physical processes may play an important role in determining the extent of spore dispersal (Gaylord et al. 2004). Kelp itself may be particularly important in this regard as drag from the fronds acts to slow down currents that pass through the forest (Jackson and Winant 1983, Jackson 1998). Consequently, spores released near the center of the forest are more likely to be retained than spores released closer to the downstream edge (Graham 2003).

Emigration via drifters occurs when wave forces rip whole plants off the bottom and ocean currents export them out of the forest. This most frequently occurs during storms, which can remove entire populations of *Macrocystis* and transport them in mass (Rosenthal et al. 1974, Dayton and Tegner 1984, Ebeling et al. 1985, Seymour et al. 1989, Edwards 2001). The percentage of drifters that successfully immigrate to new reefs and establish residency has been poorly documented; however, it is likely to be quite low. Most plants set adrift during winter storms appear to end up on the beach soon after becoming detached (ZoBell 1971, Harrold and Lisin 1989), or are transported offshore (Kingsford 1995, Hobday 2000).

Successful immigration involving drifters is not necessarily contingent upon them taking up residence at a new site. Drifters have the capacity to produce and release spores during transport, and thus they have the potential to influence the colonization of neighboring reefs by providing a localized source of spores. However, it is important to recognize that a drifting plant or plant fragment constitutes a relatively small spore source and constraints on colonization distance due to dilution effects are expected to be high, especially in the case where drifters are transported high in the water column. Such constraints argue that any colonization originating from spores released by drifters would occur in isolated patches only along the drift trajectories. Such localized recruitment contrasts greatly with the widespread, relatively uniform recruitment of *Macrocystis* that is typically observed following large disturbance events (Dayton and Tegner 1984, Dayton et. al. 1992, Edwards 2001) even at sites located relatively far from the nearest source of spores (e.g., Ebeling et al. 1985, Reed et al. 2004). For drifters to account for such widespread phenomena would seemingly require two coincident factors:

environmental conditions suitable for kelp recruitment, and either a constant supply or an adequate residence time of a large number of fecund drifters distributed over a substantial area. As far as we know such conditions have never been reported. Thus, although spore dispersal from drifters may play a valuable role in occasional long-distance dispersal events that are important for biogeographic expansion and genetic exchange, they do not appear to play a major role in rapid recolonization events, which typify the patch dynamics of giant kelp in California.

The recovery of giant kelp populations destroyed by a disturbance need not be dependent on immigration if sufficient numbers of benthic microscopic stages survive the disturbance (Dayton 1985, Kinlan et al. 2003). It has been suggested that banks of microscopic forms may function as a survival mechanism for benthic macroalgae in ways that are analogous to seed banks of terrestrial plants (Chapman 1986, Hoffmann and Santelices 1991). Under these circumstances dispersal from another patch is not necessary for explaining recolonization events because local populations have the potential to be self-replenishing even in the event of a prolonged absence of reproductive adults. Such may have been the case for *Macrocystis* near its southern limit in Baja California following its widespread disappearance during the 1997-1998 El Niño. *Macrocystis* recolonized depopulated sites where the nearest known source of spores was more than 100 km away (Ladah et al. 1999). Recruitment occurred at least six months after all adult *Macrocystis* had succumbed to poor growing conditions. The source for these recruits was assumed to be benthic microscopic stages that persisted through the adverse El Niño conditions. Such prolonged survival of microscopic kelp stages does not appear to be common in other parts of *Macrocystis'* range. Several experimental studies done in southern California indicated that microscopic stages of *Macrocystis* have a relatively short life span (typically less than a couple of weeks), and that the vast majority of recruitment originates from recently settled spores (Deysher and Dean 1986, Reed et al. 1988, Reed 1990, Reed et al. 1994, Reed et al. 1997). Moreover, dense recruitment of *Macrocystis* to newly constructed artificial reefs located several kilometers from the nearest spore source (Davis et al 1982, Reed et al.2004) provides conclusive evidence that spore immigration (whether released from attached plants on a neighboring reef, or from immigrant drifters) is a feasible means of colonization, and that the metapopulation concept is appropriate for explaining the dynamics of discrete giant kelp beds in southern California**.**

C. Spore production, release, and competency

Macrocystis is not only one of the world's fastest growing autotrophs, but it is also one of the most fecund. Spores are produced in blades termed sporophylls that are located near the base of the plant. Each sporophyll may contain as many as 10 billion spores and any given plant may produce a crop of 100 or more sporophylls at least twice per year (Reed et al. 1996, Graham 2002). Plants generally begin producing spores in their first year after attaining a size of four to eight fronds and a wet somatic mass of eight to ten kg (Neushul 1963). Spores appear to be released continuously throughout the year, with peaks occurring in early winter and late spring/early summer (Anderson and North 1967, Reed et al. 1996). Aperiodic events such as increased water motion associated with storms may accelerate the rate of spore release. Reed et al. (1997) observed a 50 % decrease in sorus area of plants immediately following a large storm.

Half of this decrease resulted from a reduction in sorus length due to sporophyll erosion which accompanies spore release (D. C. Reed unpublished data). Unlike the bull kelp *Nereocystis luetkeana,* which displays strong diel periodicity in spore release (Amsler and Neushul 1989a), *Macrocystis* shows little within-day variation in rates of spore liberation (Graham 2003). Consequently, the timing of tidal or wind-driven changes in flow that occur on a daily basis is likely to be of little importance in determining the transport of spores.

Actively swimming spores of giant kelp are typically released into the plankton within 1 m of the bottom (Gaylord et al. 2002). They can remain swimming for several days, but most stop within 24 hours, regardless of whether they reach the bottom or not (Reed et al. 1992). There is some evidence that *Macrocystis* spores have a short (i.e., several hours) pre-competency period during which time germination is impaired, should settlement occur prematurely (Reed and Lewis 1994). Such phenomena could serve to promote outcrossing and reduce the adverse effects of inbreeding depression, which in *Macrocystis* are quite severe (Raimondi et al. *in review*).

While in the plankton spores are able to maintain net positive photosynthetic rates under light conditions that are typical of the subtidal environment in which they are found (Amsler and Neushul 1991). Photosynthesis, however, is not essential for spore motility. Like many marine larvae, kelp spores contain large internal lipid reserves that serve to fuel swimming and germination (Reed et al. 1992, 1999). Energy derived from photosynthesis allows spores to conserve their internal lipid reserves and swim for a longer period of time (Reed et al. 1992). Spores that stop swimming before contacting a surface do not immediately die, but germinate in the water column and continue to grow and develop. Germinating in the water column, however, is not without costs. Although spore motility has little effect on the distance over which kelp spores are dispersed (Gaylord et al. 2002), it may greatly enhance a spore's ability to find a high quality microsite in which to settle. *Macrocystis* spores (and those of the palm kelp *Pterygophora californica*) exhibit chemotaxis towards nutrients that not only stimulate settlement, but also promote growth and development following germination (Amsler and Neushul 1989b, 1990). Hence, factors that prolong the swimming stage of spore development may increase the chances of successful settlement and recruitment, because a motile spore is better able to a select a favorable microsite than is a non-motile, planktonic germling. Perhaps more important is the increased dilution of propagules that accompanies a planktonic germling which remains in the water column for extended periods, reducing its chance of finding a mate and successfully reproducing.

D. Post-settlement processes

The production of sporophytes from gametophytes requires a complex set of biotic and abiotic conditions. Light, nutrients, temperature, and sediments need to be within critical threshold levels for gametophytes to grow and reproduce (Devinny and Volse 1978, Lüning and Neushul. 1978, Deysher and Dean 1984, 1986, Kinlan et al. 2003). The co-occurrence of these factors in southern California is unpredictable in space and time owing to variation in oceanographic conditions (Deysher and Dean 1986). Biological processes can also alter levels of light and nutrients to influence patterns of sporophyte recruitment. For example, unlike the large *Macrocystis* sporophyte that monopolizes light, microscopic gametophytes are poor competitors for light and space and readily succumb to larger and/or faster-growing algae (Reed and Foster 1984, Reed 1990). Not surprisingly, recruitment of *Macrocystis* sporophytes is typically greatest on surfaces lacking other biota (Reed and Foster 1984, Ebeling et al. 1985, Reed et al. 1997). Sporophyte production is also influenced by strong intra- and inter-specific competition of microscopic stages (Reed 1990, Reed et al. 1991). The need for spores to settle at high densities to ensure fertilization coupled with the drastic difference in size between the gametophyte and sporophyte phases essentially guarantees that strong density-dependent mortality will occur during the production of sporophytes. Additional mortality to early life stages of kelp results from grazing invertebrates and fishes, which can scour the bottom and cause patchiness in sporophyte recruitment over a range of spatial scales (Harris et al. 1984, Dean et al. 1984, Leonard 1994).

IV. Spore Dispersal

A. Factors affecting colonization distance

The distance that a spore is dispersed is determined by the length of time it spends in the plankton and the speed, direction, and timescales of variability of the currents that transport it while it is suspended. Suspension times are influenced by the height above the bottom that a spore is released, and its net sinking rate. Turbulence produced from waves and currents, wind-driven surface mixing, water stratification, shoreline bathymetry and bottom roughness all interact to influence net sinking rates of spores (Gaylord et al. 2004). In the case of small particles like kelp spores, which are nearly neutrally buoyant, turbulence acts to increase sinking rates (McNair et al. 1997). Even very slight turbulence can drastically reduce the average time it takes a spore to contact the bottom. For example, the mean suspension time for a *Macrocystis* spore released 42 cm off the bottom in still water is approximately 97 hours, but is expected to be only about 9 hours under conditions of a 2 cm s^{-1} current and 0.5 m waves, at least in regions outside kelp forests above relatively smooth sand flats (Gaylord et al. 2002). Within-forest processes will attenuate current speeds and likely reduce rates of vertical mixing, extending spore suspension times to a certain extent (reviewed in Gaylord et al. 2004). The ultimate effect of a forest on overall transport distance is less clear, however, because the degree to which the counteracting effects of slower currents and reduced mixing offset one another has not been examined in any detail. Note also that the dispersal of a spore does not necessarily end upon first contact with the bottom. Turbulent shear near the seabed may resuspend spores following their initial contact and allow them to bounce along the sea floor. Such saltation of spores may occur in *Macrocystis* because spore attachment appears to be greatly reduced in even moderate flows (~15 cm s^{-1}, Gaylord et al. 2002).

Spore dispersal distance is not the sole determinant of colonization distance in kelps. As mentioned above (see section III.A) colonization distance also depends on the size of the spore source, due to dilution effects that accompany spore dispersal. Source size is determined by the density and fecundity of the parental population, and the degree to which adults within a population release their spores in concert (Reed et al. 1997). The synchronous release of spores during conditions that promote advection may extend the distance of colonization beyond that expected in the absence of reproductive synchrony. In the case of *Macrocystis*, increased water motion during storms may trigger large pulses of spore release and promote greater dispersal (Reed et al. 1988, 1997). The importance of storms in promoting colonization extends beyond increased dispersal as storms also create bare space, which increases the likelihood of successful colonization (Dayton and Tegner 1984, Ebeling et al. 1985, Reed et al. 1997). Such episodes of storm-enhanced spore dispersal and colonization may also play an important role in the dynamics of local populations if spores that arrive during storm events contribute disproportionately more to recruitment than locally produced spores released during calm conditions. This is possible in kelps, because conditions favorable for recruitment generally follow storms, which reduce competition for light and space (Cowen et al. 1982, Dayton and Tegner 1984, Dayton et al. 1992), and promote enhanced spore settlement (Reed et al. 1988, Reed et al. 1997).

B. Empirical estimates of spore dispersal

We know of only three published accounts of dispersal in *Macrocystis*: two in which dispersal distances were inferred from observations of the density of young sporophytes at varying distances from different sized groups of adults (Anderson and North 1966, Reed et al. 2004), and one in which dispersal distance was estimated using the density of newly settled gametophytes at 0, 3, and 10 m from isolated adults (Reed et al. 1988). While these studies have helped to broaden our understanding of dispersal in *Macrocystis,* limitations in their temporal and spatial resolution render them inadequate for determining the extent to which dispersal varies in time and space. Such information is needed to determine levels of connectivity among local kelp populations.

We recently collected data on water motion simultaneously with data on spore dispersal using two different experimental designs to obtain a more comprehensive understanding of spore dispersal in *Macrocystis* and the processes that affect it. One study involved estimating dispersal from individual adult sporophytes, while the other entailed estimating dispersal from an experimental population of adult sporophytes. Both experiments were done on a nearly flat area of sandy bottom at 10 m depth, near Carpinteria, CA, that was at least 1 km away from the nearest *Macrocystis* patch. Having an isolated spore source is key to obtaining empirical estimates of spore dispersal because it allows one to investigate dispersal distances from the nearest known source of spores without interference from neighboring spore sources. We estimated dispersal from individual adults by transplanting three mature sporophytes 50 meters apart from each other in a line perpendicular to shore. On 60 dates between January 1998 and April 1999 we recorded the densities of recently settled spores (i.e., gametophytes) on arrays of ground glass microscope slides placed north, south, east and west of each of the three sporophytes. Slides were positioned approximately 15 cm above the bottom on a PVC post anchored in the sand at distances of 0.5, 1, 5, and 10 m from each sporophyte. Additional slides were placed 50 meters east and west of the inshore and offshore sporophytes in the array to detect any dispersal over longer distances. In the second study, the experimental population of *Macrocystis* used to examine dispersal from a larger group of fertile individuals was created by transplanting 64 adult sporophytes in a uniform array (i.e., spaced 3 m on center) to a 25 x 25 m area. Spore settlement in this experiment (hereafter referred to as the kelp bed experiment) was recorded on microscope slides positioned 3, 6, 12, 18, 24, 48, 72, 96, and 120 m north, south, east and west of the edge of the sporophyte array on 29 dates between June and September 1999. Slides used to collect newly settled spores in both experiments were placed in the field for two to three days, collected, transported to nearby laboratory facilities and sampled for spore settlement as described in Reed et al. (1988).

When averaged over all trials, spore settlement decreased with distance as a negative power function in both the individual sporophyte and kelp bed experiments (Figure 6). These general patterns of spore dispersal are similar to those described for *Macrocystis* in earlier studies (see references cited above). To explore spatial and temporal patterns of spore dispersal, we used nonlinear regression analysis to estimate dispersal as a function of distance for each trial in each of the two experiments. The equations produced from these regressions were used to calculate the x intercept, which represents an estimate of the maximum distance that spores dispersed in a given trial. These maximum values were then used to produce frequency distributions for each experiment, showing the percentage of trials in which spore dispersal extended out to different distances (Figure 7). Results indicate there was a greater range in dispersal among trials in the experiment involving individual plants than in the kelp bed experiment. Dispersal in 70% of trials involving individual plants did not exceed 16 meters, whereas in 5% of trials it was estimated to be > 2000 meters. By contrast, maximum dispersal in nearly all trials from the kelp bed experiment ranged between 80 to 500 meters. This difference may have been due in part to differences in the level of spatial resolution in estimates of dispersal distance, particularly in the case of the individual plant experiment where we projected dispersal far beyond our maximum sampling distance (50 meters). Perhaps more importantly, trials for the individual plant experiment were done over a 15-month period that encompassed a wider range of oceanographic conditions than did the three-month kelp bed experiment that was done during a calm summer period (Table 1). The two variables expected to have the most influence on spore dispersal are currents and waves (Gaylord et al. 2002), both of which were lower in the kelp bed experiment compared to the individual plant experiment.

C. Modeled estimates of spore dispersal

Gaylord et al. (2002) developed a physically-based model for dispersal of macroalgal spores, with specific reference to *Macrocystis*. This model linked wave and current conditions to a boundary layer model of turbulence enabling prediction of profiles of vertical mixing in nearshore habitats. A random walk approach was used in conjunction with the profile of vertical mixing and the rate of spore sinking to simulate the vertical movement of spores following their release from a given height above the bottom, and to estimate the time required for them to first contact the seafloor. An estimate of the dispersal distance was obtained by multiplying the time for a spore to reach the bottom by current speed. This approach provided a rough estimate of the distances spores are transported before first contacting the bottom for fixed wave and current conditions.

Flows in nature, however, are not constant and the general construct described above cannot be expected to accurately predict dispersal distances at specific locations or times. To address this complicating factor, we extended the Gaylord et al (2002) approach to account for variation in flow caused by oscillating currents, which change speed and direction over time. Although one could also incorporate variation in wave height and wave period, such measurements are not as readily available, and as shown in Gaylord et al. (2002), are likely to play a lesser role than currents in determining dispersal distances. Our approach in predicting spore dispersal therefore proceeded as follows. First, we computed the shear velocities corresponding to a range of current and wave conditions in 10 m of water that interact with a seabed characterized by a physical roughness height of 0.08 m, as in Gaylord et al. (2002). Second, we assumed a release of 1000 spores every two hours. Third, we tracked the position of these spores until they first contacted the bottom using the random walk approach described above, but with changing flow conditions updated every 20 min. This included updating shear velocities that were dictated by wave and current conditions. We repeated this three-step process using current data from two 30-day periods: January 15 - February 15, 2002 and June 1-30, 2002, corresponding to the winter and late spring / early summer peaks in spore release exhibited by *Macrocystis* in southern California (Reed et al. 1996). To simulate better the transport velocity that sweeps suspended spores horizontally near the bottom, we incorporated a linear decrease in current speed in the lowermost 1 m of the water column. This follows from the observation that the velocity profile in the lower 10 percent of a boundary layer is usually logarithmic (Schlichting, 1979, Grant and Madsen 1986), which approaches a linear gradient for small distances above the seafloor. Because waves are typically largest in the winter in southern California, we assigned a wave height of 1.0 m in winter (January – February) and 0.5 m in June, both with a 10 s period. As noted above, waves were held constant within each 30-day period.

We used data on current speed from two shallow reefs in the Santa Barbara Channel that experience different flow regimes to model temporally varying currents: Carpinteria Reef, located in about 12 m water depth, and Naples Reef located in about 17 m depth (Figure 1). Giant kelp forests commonly occur on both reefs. Currents at both sites were measured from bottom-mounted acoustic Doppler current profilers (ADCPs) placed at the outside edge of the forests at each site as part of the ongoing Santa Barbara Coastal Long Term Ecological Research program. Current data from the ADCPs were averaged into 1 m bins that extended from about 2 m above bottom up to about 1- 2 m below the surface, depending on wave conditions. Current velocities were recorded at two-minute intervals, and then averaged to 20-minute intervals for use in the dispersal model. Currents at the two sites flow approximately parallel to isobaths and parallel to the coastline, which runs roughly east west (Figure 1). Currents were averaged vertically and then rotated into principal axis directions for the dispersal model. The major principal axes at both sites are oriented parallel to isobaths so hereafter this is referred to as the alongshore direction (positive approximately eastward). Similarly, the minor principal axis was taken to be the across-shore direction (positive onshore, or approximately northward). Along-shore currents were used in the model because they are much stronger than across-shore currents at both sites (data not shown). Furthermore, currents in shallow water tend to flow parallel to isobaths (e.g., Pedlosky, 1987) so this is likely to be the dominant direction for spore dispersal.

Along-shore currents at both sites vary strongly on a wide range of time scales, but exhibit prominent tidal fluctuations: at Carpinteria Reef tidal fluctuations are semi-diurnal while at Naples Reef they are diurnal (data not shown). Tidal fluctuations often cause reversals of along-shore currents at both sites, particularly in winter. In summer, current reversals are less common because coastal sea level changes typically force strong westward flow along the mainland coast of the Santa Barbara Channel (Harms and Winant, 1998).

Histograms of along-shore currents show that current speeds were on average two to three times faster at Naples Reef compared to Carpinteria Reef, and were generally higher in June compared to January/February (Figure 8). Currents were on average two to three times faster at Naples Reef compared to Carpinteria Reef. Maximum current speeds were westward at ~0.4 m s^{-1} at Naples Reef, but only ~0.2 m s^{-1} at Carpinteria Reef. .The histograms also show the predominance of westward flow, especially in June. Current speeds experienced by most giant kelp populations in southern California are likely to fall within the range encompassed by these two sites and time periods.

The patterns of spore dispersal predicted from our model reflect differences in current speed distributions observed between the two sites and seasons (Figure 9). Of the four model runs, dispersal was predicted to be greatest for Naples Reef during June and shortest for Carpinteria during January/February. The more persistent westward flow at both sites probably accounts for the greater dispersal distances in June; more symmetric current speed distributions probably account for smaller dispersal distances in January/February. Median dispersal distances ranged between 40 m for Carpinteria in January/February to 400 m for Naples in June; ten percent of all spores (i.e. the 90th percentile of the spore dispersal distribution) dispersed approximately 1 km at Carpinteria in January/February and 4 km at Naples in June before first contacting the bottom. These values are of the same general magnitude as those derived from our empirical studies discussed above.

V. Connectivity among local populations

Variability in simulated and empirical distributions of spore dispersal suggests that connectivity among discrete patches of *Macrocystis* – and hence the metapopulation dynamics of giant kelp forests – may be strongly influenced by local oceanographic conditions. To examine the connectivity of discrete patches of *Macrocystis* in southern California, we combined dispersal simulations based on the four oceanographic scenarios modeled above (i.e., Carpinteria Reef and Naples Reef in January/February and in June) with the 34-year monthly time-series of patch extinction/recolonization described above (see Section II.). Average distances between neighboring patches varied from 0.5 to 14 km, with 80% of all patches occurring within 2 km of another patch (Figure 10a). Since each patch may have multiple neighbors, a richer description of spatial structure can be gained by considering the number of neighbors encountered as a function of distance from a patch. In southern California, patches have on average relatively few (~ 1 to 3) neighbors within 10 km; the number of neighboring patches increases rapidly in neighborhoods greater than 10 km in size (Figure 10b).

The distribution of distances among all possible combinations of patches of giant kelp in southern California ranges from hundreds of meters to hundreds of kilometers (Figure 9, dashed line). When our simulated spore dispersal profiles are overlaid on this pattern, we find that the level of potential connectivity among all patches (i.e., the probability that any two randomly selected patches in southern California are directly connected by spore dispersal) ranged from 0.37% to 1.58 %, depending on the specific current regime (see overlap between the distributions of dispersal distance [solid lines] and inter-patch distance [dashed line] in Figure 9).

Estimates of the proportion of propagules dispersing a given distance before first contacting the bottom provide only a crude measure of the actual level of connectivity among discrete patches. More accurate measures of the degree of connectivity require information on the absolute numbers of propagules that are exchanged between neighboring patches and on their probability of survival following settlement. This is particularly important in kelps because their spores need to settle at high densities to ensure subsequent reproduction (see Section III.A.). Obtaining information on absolute estimates of spore exchange rates for *Macrocystis* is difficult for a number of reasons. The models of dispersal presented here assume spores settle at first contact with the bottom, but saltation after primary contact could substantially extend dispersal (Gaylord et al. 2002). The degree to which this occurs in nature, however is unknown. Moreover, the probability of reproductive success for spores that have spent long periods in the water column, particularly those that have stopped swimming and/or germinated, is poorly understood, as are the chances of reproduction between different-aged gametophytes. All of these processes could influence the "effective" dispersal distance of kelp spores in nature, and deserve further detailed study.

As noted above (Section III.A.) the density of spores that settle at a given distance from their point of release is proportional to the size of their parental spore source. Our modeled estimates of connectivity assume that spore sources (i.e., the standing crop of spores in a patch) are spatially and temporally homogenous. Clearly this is not true, and our values of connectivity may be underestimated in the case of large and/or continuous spore sources, and overestimated in the case of small and/or sporadic spore sources. The effects of variation in the size of the spore source on the level of connectivity can be evaluated to some extent by examining connectivity under different threshold levels of spore dispersal. The rationale here is that a larger proportion of spores will settle at densities sufficient for fertilization when released from a large spore source compared to a smaller spore source. Other factors influencing spore source strength include the abundance and per capita fecundity of adult plants (Graham 2003, Reed et al. 2004), the degree to which they display synchrony in spore release (Reed et al. 1997) and oceanographic conditions affecting dilution during transport (Gaylord et al. 2004). Thus a dispersal threshold defined by the 50th percentile of the spore dispersal distribution could be viewed as representing connectivity to a relatively small/weak spore source, whereas a larger/stronger spore source might result in connectivity at distances reached by only 10% of spores (i.e., the 90th percentile of the dispersal distance distribution)

Figure 11 shows frequency distributions of average connectivity (i.e., number of neighboring patches connected via dispersal) for different dispersal thresholds, defined by using percentiles of the dispersal distance probability distribution. Depending on site, season, and the dispersal threshold chosen to define connectivity, an average patch of *Macrocystis* may be completely isolated or have up to 4 or 5 connected neighbors. For example, during June conditions at Carpinteria Reef, 10% of spores (equivalent to a cutoff percentile = 90%) were estimated to disperse at least $x_c = 2.4$ km (Figure 11). Under these conditions, 42% of patches would exchange spores with 1 other patch and 5% of patches would exchange with 4 other patches; 19% would not exchange spores with any other patches. Higher current speeds, such as for June conditions at Naples, would result in exchanges among more patches. That the level of connectivity was highly sensitive to the choice of the threshold dispersal rate argues that connectivity among discrete patches of giant kelp depends greatly on factors affecting the strength of the spore source (e.g., the standing crop of spores in a patch) as well as the spacing among patches. Thus spatial and temporal patterns of adult fecundity in giant kelp may influence regional patterns of colonization in much the same manner as has been found for acroporid corals in the Great Barrier Reef (Hughes et al 2000).

VI. Conclusions

Our analyses of local extinctions, colonization, and immigration (via spore dispersal) suggest that the metapopulation concept is likely to prove useful in explaining the population dynamics and genetic structure of *Macrocystis*. Limitations on dispersal in giant kelp appear to prevent patches within a region from behaving as a single large population. However, while most patches within a region are not directly linked, neither are they completely isolated. The average kelp bed in southern California appears to be connected to one to three neighboring kelp beds via spore dispersal for a relatively wide range of oceanographic conditions. Importantly, connectivity even among nearby patches seems to be mediated by spores that travel far beyond the median dispersal distance (i.e., 75th – 90th percentile; Figure 11); that is, a relatively small fraction of dispersing spores accounts for a disproportionate amount of inter-patch connectivity. As a result, persistence of a giant kelp metapopulation depends on the tails of the dispersal curve and cannot be predicted simply from the average or median dispersal distance. This result is consistent with theoretical predictions that (re)colonization and population spread are highly dependent on the tails of a dispersal distribution (Kot et al. 1996), but contrasts with results for stable environments where persistence is relatively insensitive to the tails of the dispersal curve (Lockwood et al. 2002).

Patch size, fecundity and proximity to neighboring patches undoubtedly exert strong influences on the level of connectivity among patches. Environmental stochasticity arising from biotic and abiotic disturbances appears to be the primary force driving extinctions and recolonizations of giant kelp populations in southern California. Local extinctions caused by recruitment failure (i.e., demographic stochasticity) to our knowledge have not been reported for giant kelp. This may be due in part the high capacity of giant kelp forests to produce and retain large numbers of spores, which allows for self replenishment. The relative contributions of self-seeding and spore immigration to population persistence in giant kelp is unknown and warrants further investigation.

That the vast majority of extinction events in our 34-year study period persisted for less than two years indicates that recruitment failure in unoccupied patches is a short-term phenomenon and the immigration of spores from neighboring patches is a common occurrence. The scenario revealed by our analyses suggests that giant kelp in southern California is a spatially structured metapopulation in which exchange occurs primarily between neighboring patches and is strongly influenced by patch size, fecundity (i.e., spore standing crop), spatial arrangement, and oceanographic conditions. Because giant kelp populations are distributed in a narrow depth range along the coastline, and because nearshore currents (the dominant mechanism for dispersal) flow primarily alongshore, the “stepping stone” exchange among neighboring patches is approximately one-dimensional. Such limitations on connectivity, coupled with large geographic gradients in environmental conditions likely accounts for the ecotypic variation observed for *Macrocystis* in California (Kopczak et al. 1991).

Compared with many terrestrial habitats the aqueous medium through which kelp propagules disperse is relatively unstructured. Moreover, unlike passively dispersed kelp spores and drifters, immigrants in many terrestrial metapopulations exhibit complex behavioral interactions with the heterogenous landscape that influence connectivity between patches. However, it is important to recognize that the physical properties of the nearshore ocean are not devoid of spatial and temporal structure, and certain areas or times may be subjected to currents and waves that are more conducive to promoting connectivity than others. Indeed, our analyses of connectivity involving Naples and Carpinteria Reefs indicate this to be the case. Thus the nearshore habitat where kelp occurs may represent a more dynamic analogue of the terrestrial concept of a landscape matrix (Weins 1977). Perhaps even more important to the metapopulation structure and dynamics of giant kelp are the effects of a heterogenous environment on the ability of immigrants to become established, grow, and reproduce. Shallow reefs may differ greatly from each other in habitat quality due to differences in topography, wave exposure, sedimentation, nutrients and other geophysical and chemical properties. Differences in colonization success, growth, and reproduction among patches of different quality may greatly affect the magnitude of "effective" connectivity between patches.

Our estimates of spore dispersal when viewed in the context of the size and distribution of discrete patches suggest that many local populations of *Macrocystis* in the Southern California Bight are "on the edge" with respect to connectivity. Relatively small increases in distances between patches could lead to substantial increases in demographic isolation. This is of particular concern because the last century has seen an increase in the average distance between reefs potentially habitable by giant kelp, due in part to anthropogenic impacts including substrate burial and reduced water clarity near major ports, warm water effluent from generating stations, and municipal sewage outfalls (Crandall 1912, Harger 1983, Wilson and North 1983, Schroeter et al. 1993, Bence et al. 1996). Continued changes in the configuration of nearshore habitat suitable for giant kelp forests in this region will likely present severe challenges for conservation, persistence, and local adaptation/evolution of giant kelp populations. However, because the level of connectivity among patches is strongly dependent on the length of the "effective" dispersal tail, additional research is needed to determine the amount of dispersal that constitutes connectivity, which broadly defined includes spore dispersal, settlement, and post-settlement success.

The strong dependence of giant kelp connectivity and patch dynamics on environmental factors such as geomorphology (distribution of rocky substrate) and oceanography (wave disturbance and nutrient stress), suggests that the metapopulation structure of this species is likely to differ substantially among regions. For example, populations along stretches of the coast of Baja California, Mexico are far more isolated than any of the patches we studied, whereas central California kelp populations occur in a near-continuous band throughout much of the region. A better understanding of regional variation in metapopulation structure may help to explain observations of extreme variation in peristence and dynamics of this species across its global range (reviewed in North 1994).

Finally, we note that because our approximations of patch extinction and recolonization suffer from methodological limitations that could lead to either over- or under-estimates (see Section II), actual connectivity may be somewhat different from that suggested by our analyses. For example, our modeling did not incorporate cross-shore flows or dilution due to lateral mixing, two poorly understood processes that probably limit effective dispersal distance and thus reduce connectivity among patches. A detailed examination of these and other potential limitations of our analyses are beyond the scope of this chapter. Clearly, further research is needed to better characterize extinction and colonization at large scales using high-resolution mapping, as well as to more accurately quantify the effects of spore saltation, delayed recruitment, variation in the number, spacing, and fecundity of plants within a patch, and various physical processes (e.g., variability in waves and turbulence) on the effective colonization distance of giant kelp. Studies of population genetics may prove useful in this regard. The estimates of connectivity presented here provide a platform for future studies on the metapopulation ecology of giant kelp and other seaweeds.

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Table 1: Mean, minimum and maximum values for currents and significant wave height for the individual plant and kelp bed experiments. Mean currents were calculated over the duration of each experiment

	Current velocity (cm / s)		Significant wave height (m)	
	Individual	Kelp bed	Individual	Kelp bed
Minimum	0.001	0.04	0.323	0.273
Maximum	8.007	1.797	1.172	0.801
Mean	1.075	0.413	0.697	0.501

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Figure legends

Figure 1. Map of the mainland coast of southern California, depicting giant kelp canopy detected by aerial infrared photography in 1989, 1999, and 2002 (black shading) and administrative kelp bed units (outlines) assigned by the California Department of Fish and Game (CA DFG). Inset: Detail of three discrete patches of giant kelp (different shades of gray) identified according to the criteria described in Section II. These patches are separated by > 500 m at their closest point. Note that a single administrative bed may contain multiple patches, and patches can extend across administrative bed boundaries. Patches are considered to "belong" to the bed in which the majority of surface canopy falls. (Original data from CDFG, composite map and patch classification from B. Kinlan, unpublished data).

Figure 2. Percent of giant kelp patches along the mainland coast of southern California (n = 69 patches) occupied on a monthly basis from January 1968 to October 2002 as estimated from surface canopy observations made during aerial over flights.

Figure 3. Monthly rates of (a) extinction and (b) recolonization of giant kelp patches along the mainland coast of southern California, based on a 34-year monthly time series of surface canopy biomass. Bin size = 0.04, ticks denote lower edges of bins.

Figure 4. Duration of patch extinctions and patch persistence of giant kelp along the mainland coast of southern California based on a 34-year monthly time series of surface canopy biomass. Upper panels (a, b) show histograms of the average extinction and

persistence time for *n*=69 discrete patches. Lower panels (c, d) show the durations of all extinction and persistence intervals observed during the 34-year study, revealing extremely long and extremely short extinction and persistence intervals not reflected by the averages in (a) and (b).

Figure 5. Monthly probabilities for: (a) patch extinction vs. patch size, (b) patch extinction vs. patch isolation, (c) patch recolonization vs. patch size, and (d) patch recolonization vs. patch isolation. Data are from 69 discrete patches of giant kelp observed from 1968 – 2002 along the mainland coast of southern California. Patch size is defined as $L_i = \sqrt{A_i}$, where A_i is the area of patch *i* in km^2. Patch isolation is defined as the inverse-distance-weighted average size of surrounding patches that are occupied in any given month, averaged over all $T = 418$ months,

$I_j = \frac{1}{T} \cdot \sum_{t=1}^{T} \left[\left(\sum_{i \neq j} L_i \cdot \frac{1}{D_{i,j}^2} \right) \Big/ \left(\sum_{i \neq j} \frac{1}{D_{i,j}^2} \right) \right]$, where $D_{i,j}$ denotes the linear distance between occupied patches *i* and *j*. Note that low values of the patch isolation index correspond to a high degree of isolation (indicated by arrow). Lines show fitted least-squares regressions, (a) p(extinction) = -0.0316 × √(patch area) + 0.0708; (b): ln[p(extinction)] = -0.8643 × ln(isolation) – 4.7217; (c): p(colonization) = 0.0349 × √(patch area) + 0.0644; and (d): p(colonization) = 0.0760 × (isolation) + 0.0544. r^2 and *p* values for regressions are as shown.

Figure 6. Spore settlement density as a function of distance from the spore source for (a) the individual plant experiment and (b) the experimental kelp bed. Data are means (± 1

SE) of spores averaged across all trials. Note difference in the scale of the vertical axes of (a) and (b).

Figure 7. Inverse cumulative frequency distribution of dispersal distances for both the individual plant and kelp bed experiments. Shown are the probabilities that the maximum estimated dispersal in a trial occurred to distance (X) or less.

Figure 8. Histograms of alongshore (principal axis) current speeds at Naples Reef (solid lines) and Carpinteria Reef (dashed line) for two 30-day periods in 2002. Westward currents are to the left of zero and eastward currents are to the right. (a) 15 January – 15 February. Mean ± SD = 0.12 ± 0.05 m s^{-1} and 0.04 ± 0.03 m s^{-1} for Naples Reef and Carpinteria Reef, respectively. (b) 1-30 June. Mean ± SD = 0.13 ± 0.09 m s^{-1} and 0.06 ± 0.05 m s^{-1} for Naples Reef and Carpinteria Reef, respectively.

Figure 9. Dispersal potential of giant kelp spores vs. distance between discrete patches. Spore dispersal distributions (solid lines) were simulated on the basis of measured currents at Carpinteria (squares) and Naples Reef (circles) from 1-30 June, 2001 (open symbols) and 15 Jan - 15 Feb, 2001 (closed symbols) (see text for details). Left-hand vertical axis indicates the probability of dispersing at least as far as the distance on the horizontal axis. The distribution of distances between patches (dashed line) was calculated from distances between all pairs of occupied patches in all months of the study period (*n=418* months). The right-hand vertical axis indicates the percentage of distances between patches that were less than the distance on the horizontal axis.

Figure 10. Spatial distribution of *Macrocystis* patches along the mainland coast of southern California. (a) Mean distance to the nearest occupied neighboring patch, calculated for all patches in the region (*n*=69 patches) averaged over the 418-month study period. (b) Mean number of occupied patches (vertical axis) within a given radius of a patch (horizontal axis), averaged over the 418-month study period. Dashed lines indicate ± 1 SD.

Figure 11. Estimated connectivity of giant kelp patches along the mainland coast of southern California for the four simulated current regimes (columns) and for three spore dispersal scenarios (rows). Connectivity is defined as the number of occupied patches within the effective dispersal distance of a source patch. Spore dispersal was simulated under the current regimes measured at two sites (Carpinteria Reef and Naples Reef) and two seasons (15 Jan - 15 Feb 2001, 1 June - 30 June 2001). Different spore dispersal scenarios (which may correspond to variation in patch size, fecundity, degree of synchrony in spore release, and diffusive dilution) are simulated by choosing effective dispersal distances (x_c) ranging from the 50th to the 90th cutoff percentiles of the four spore dispersal profiles. Values reported are averages for $n = 69$ patches calculated over the 418-month study period.

Figure 1

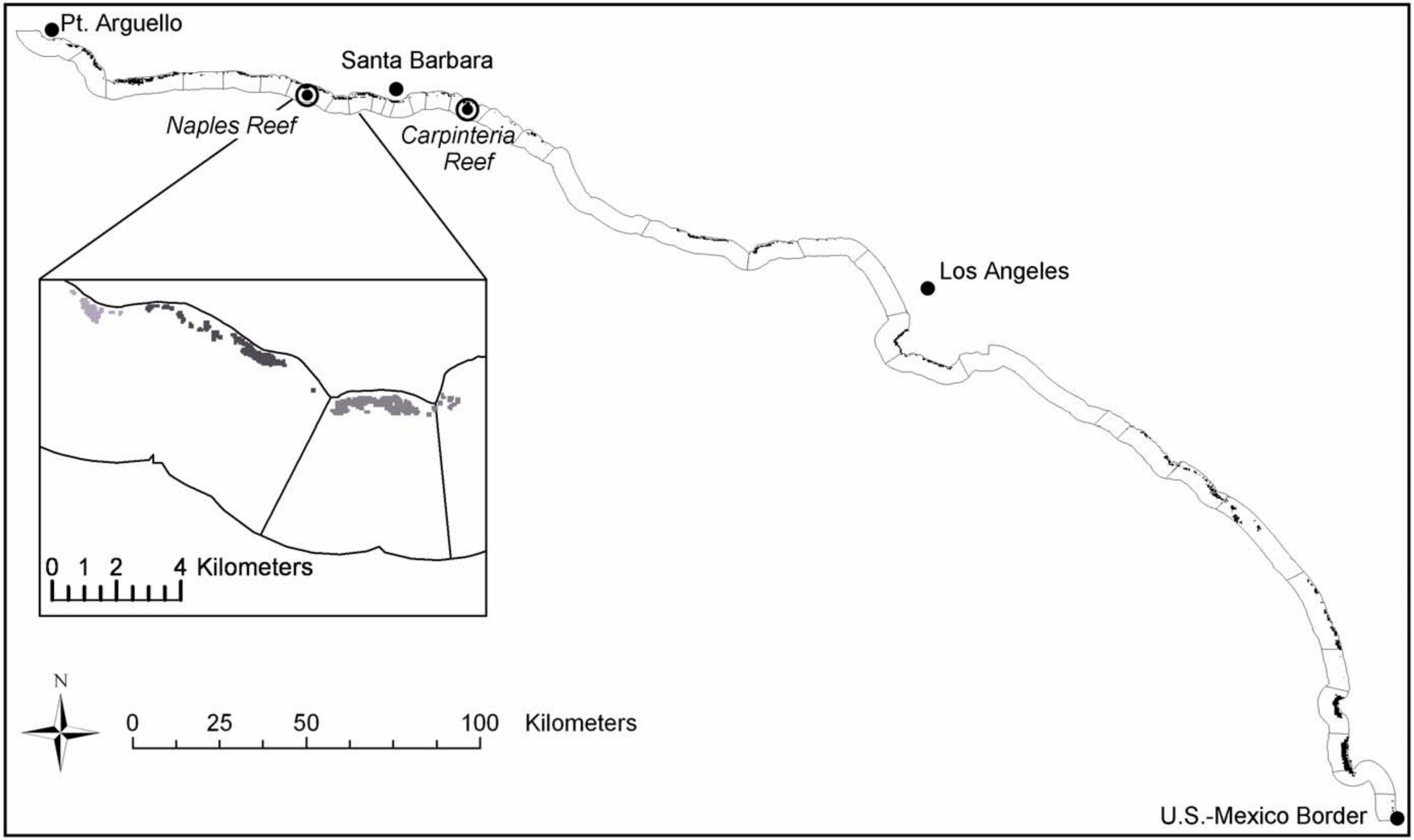

Pt. Arguello
Santa Barbara
Naples Reef
Carpinteria Reef
Los Angeles
U.S.-Mexico Border
0 1 2 4 Kilometers
N
0 25 50 100 Kilometers

Figure 2

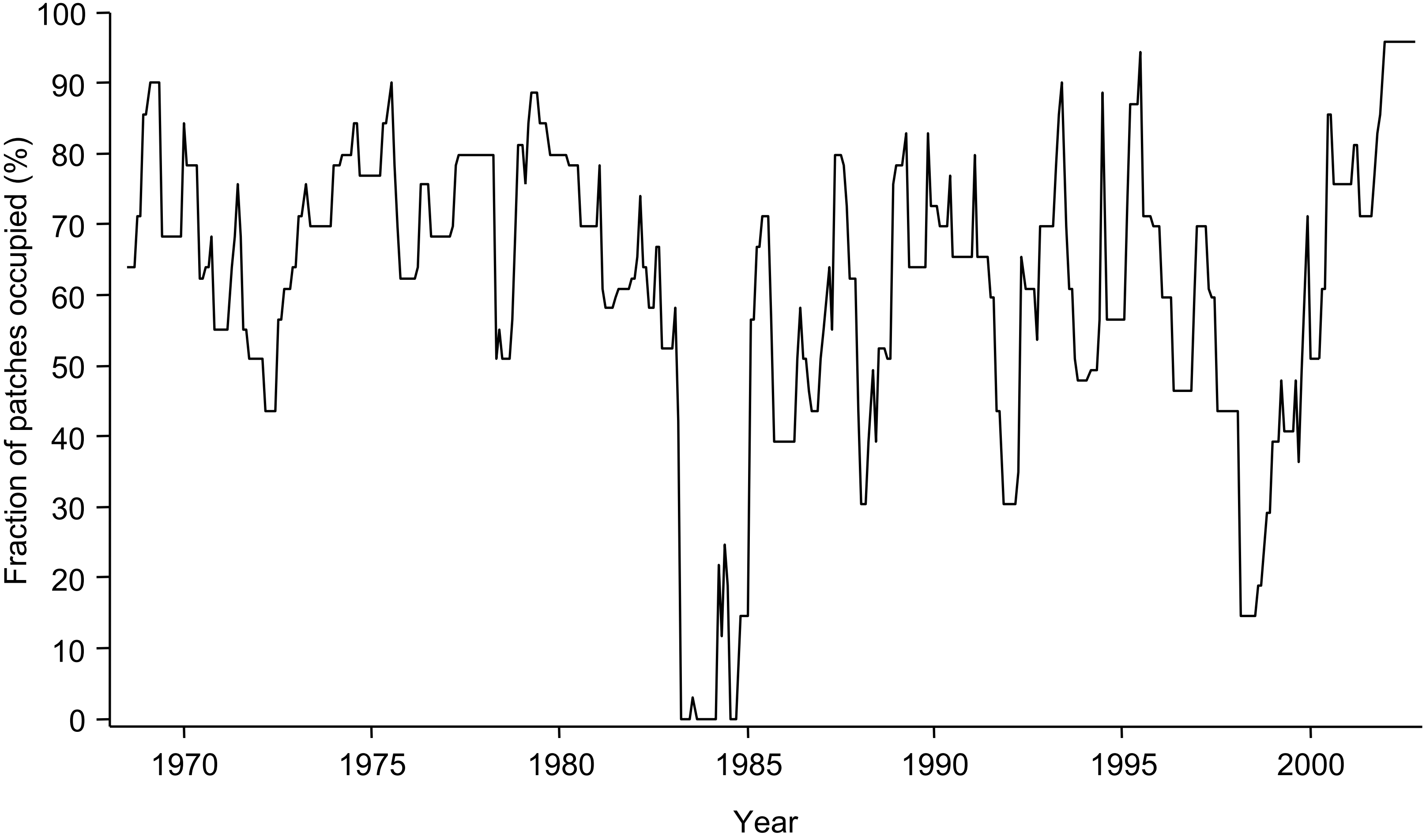

Fraction of patches occupied (%)
0
10
20
30
40
50
60
70
80
90
100
1970
1975
1980
1985
1990
1995
2000
Year

Figure 3

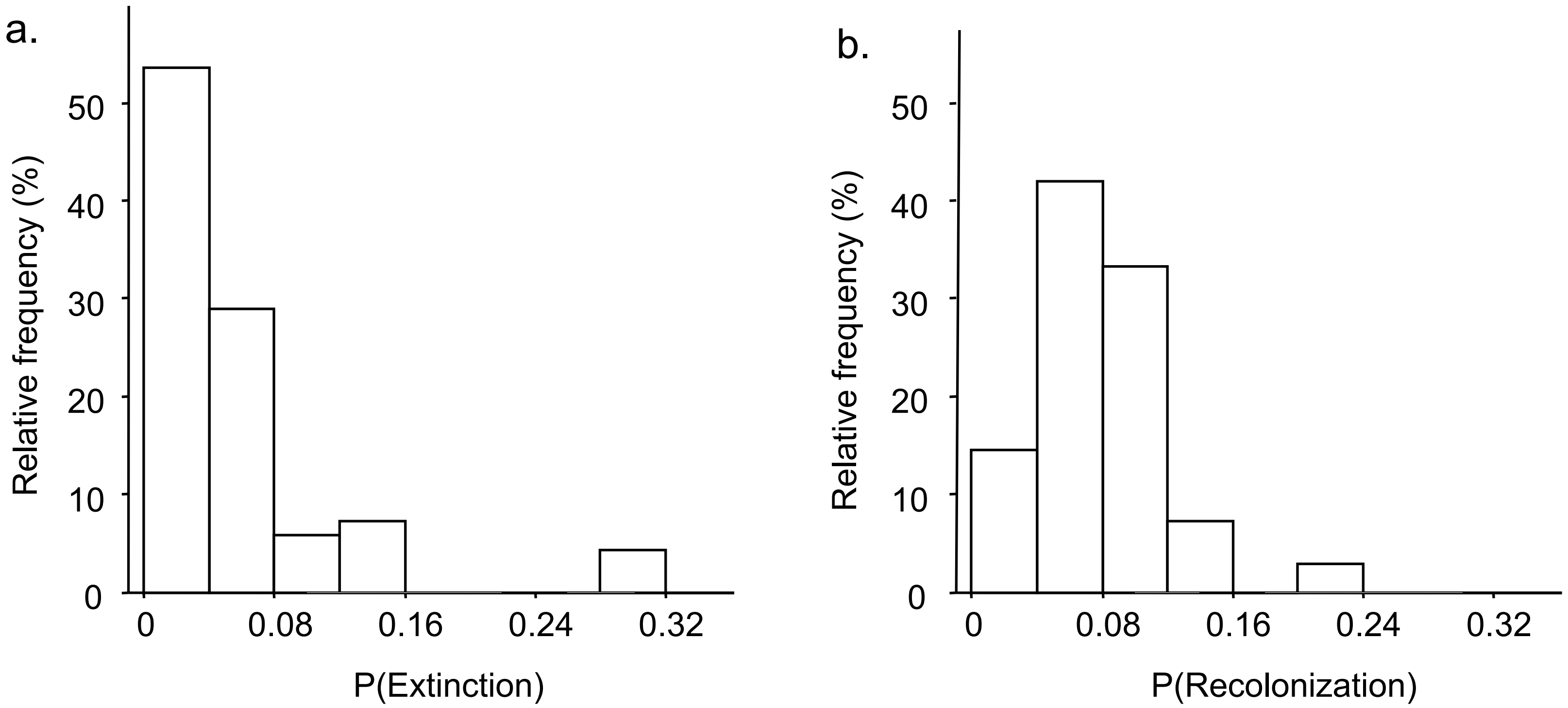

a.
Relative frequency (%)
0
10
20
30
40
50
0
0.08
0.16
0.24
0.32
P(Extinction)
b.
Relative frequency (%)
0
10
20
30
40
50
0
0.08
0.16
0.24
0.32
P(Recolonization)

Figure 4

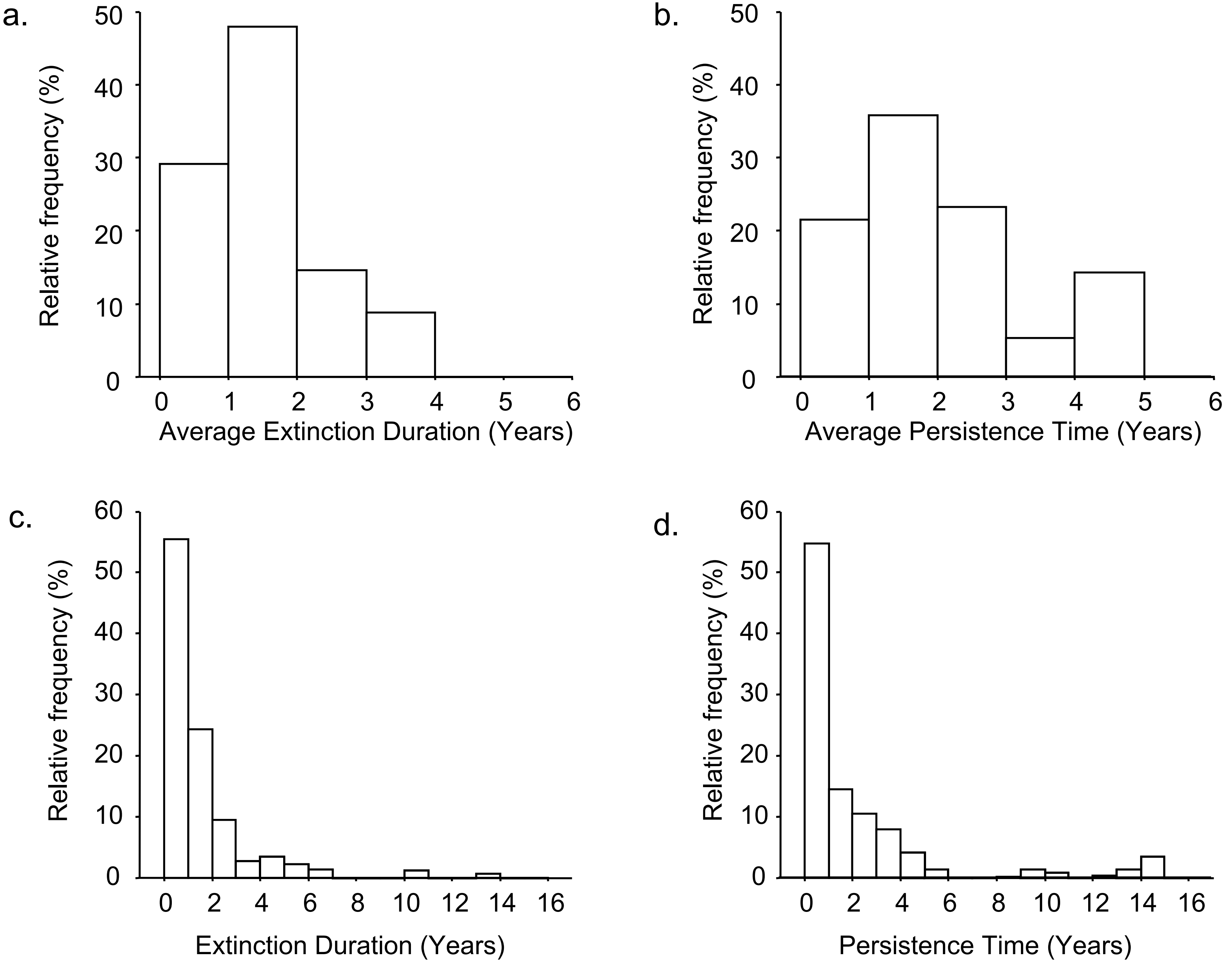
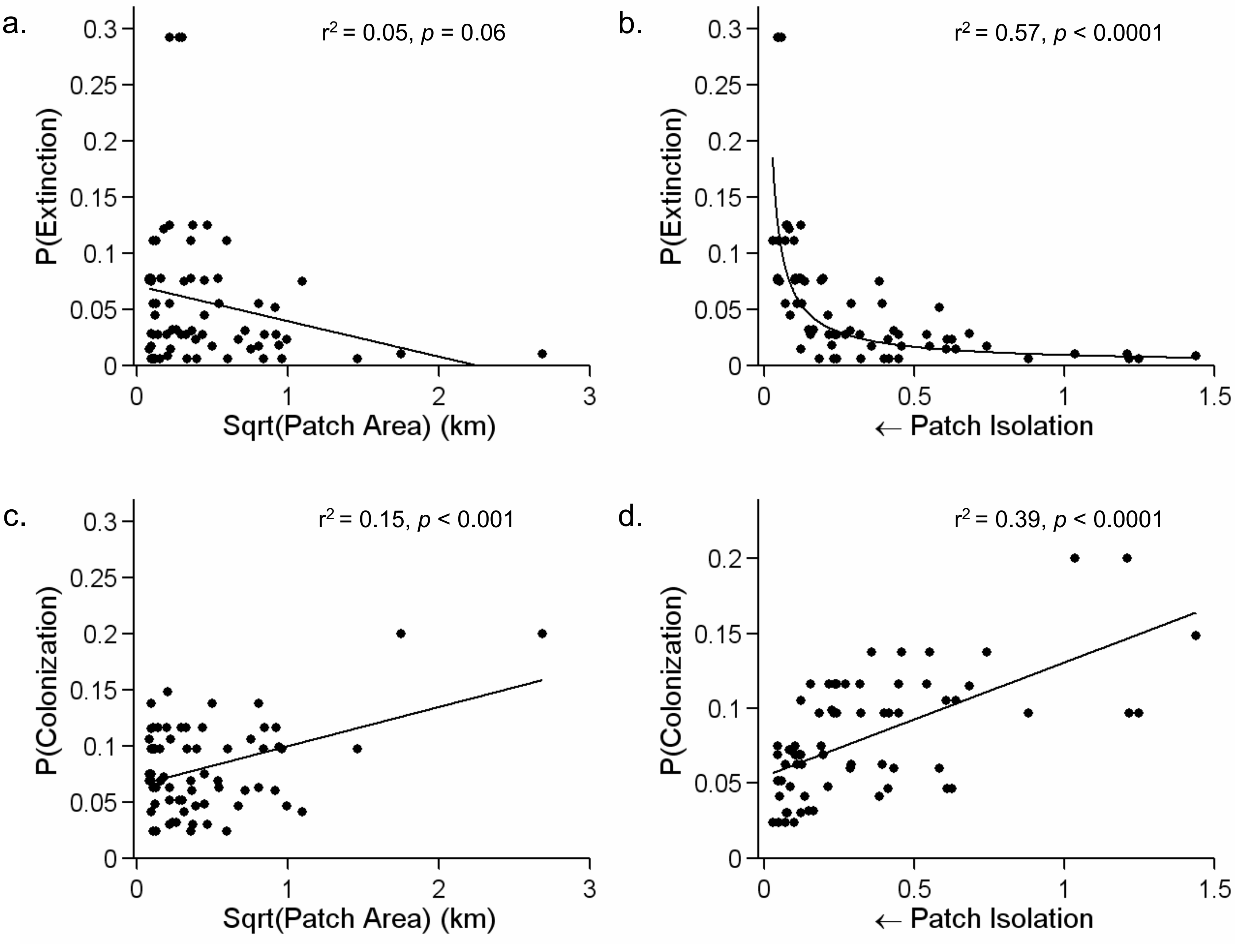
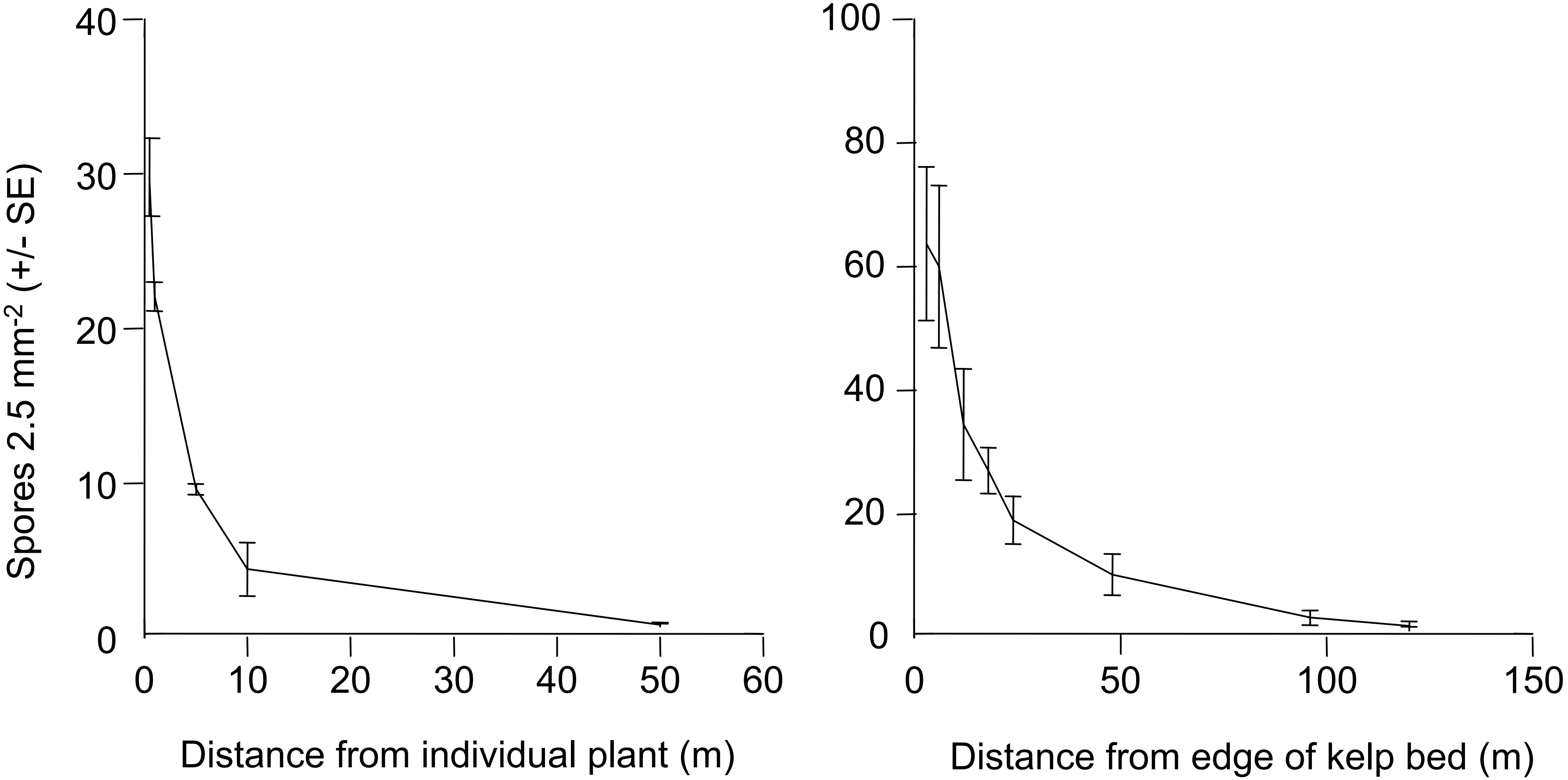

a.
Relative frequency (%)
0
10
20
30
40
50
0
1
2
3
4
5
6
Average Extinction Duration (Years)
b.
Relative frequency (%)
0
10
20
30
40
50
0
1
2
3
4
5
6
Average Persistence Time (Years)
c.
Relative frequency (%)
0
10
20
30
40
50
60
0
2
4
6
8
10
12
14
16
Extinction Duration (Years)
d.
Relative frequency (%)
0
10
20
30
40
50
60
0
2
4
6
8
10
12
14
16
Persistence Time (Years)

Figure 5



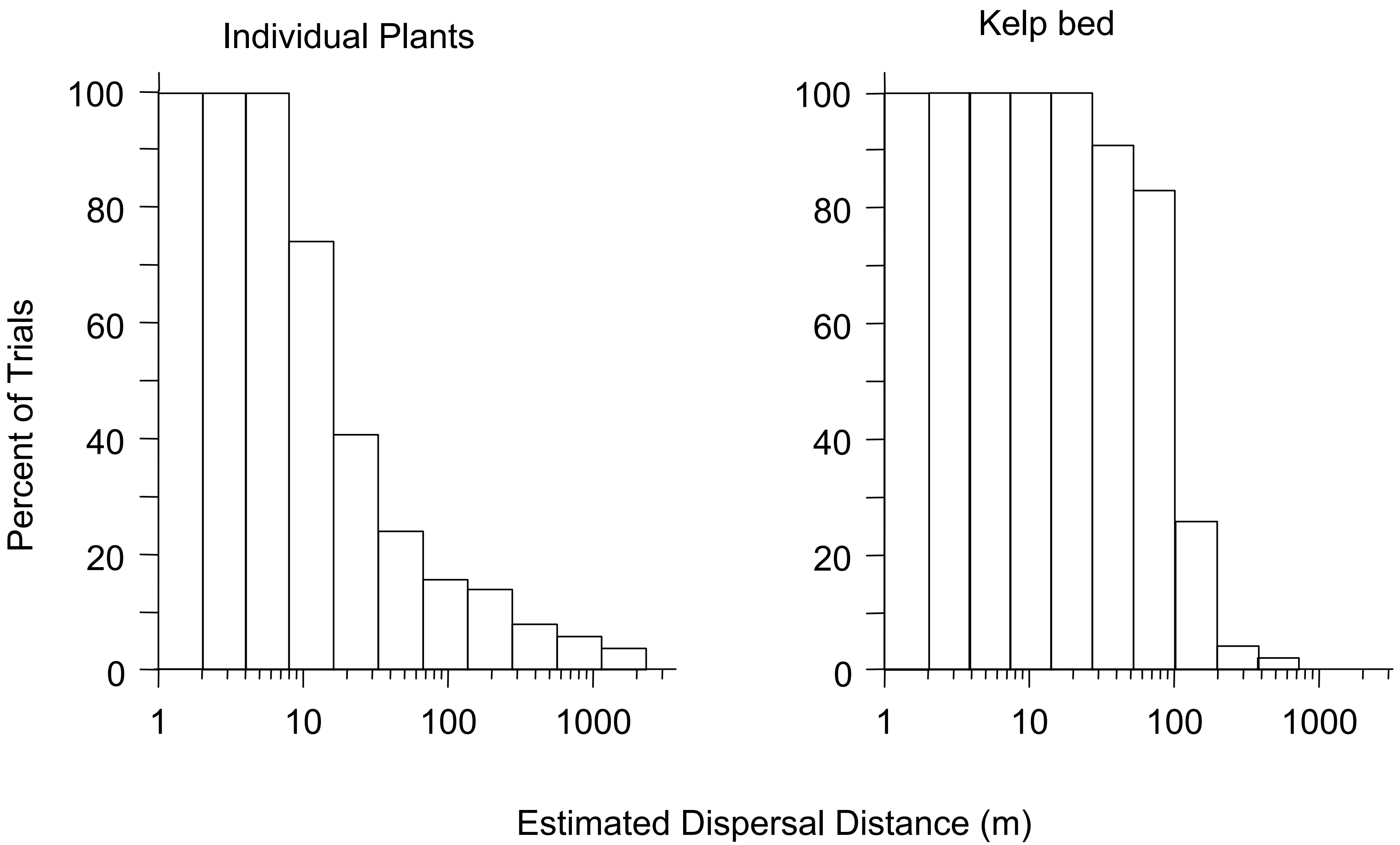
a.
$r^2 = 0.05$, $p = 0.06$
P(Extinction)
0.3
0.25
0.2
0.15
0.1
0.05
0
0
1
2
3
Sqrt(Patch Area) (km)
b.
$r^2 = 0.57$, $p < 0.0001$
P(Extinction)
0.3
0.25
0.2
0.15
0.1
0.05
0
0
0.5
1
1.5
← Patch Isolation
c.
$r^2 = 0.15$, $p < 0.001$
P(Colonization)
0.3
0.25
0.2
0.15
0.1
0.05
0
0
1
2
3
Sqrt(Patch Area) (km)
d.
$r^2 = 0.39$, $p < 0.0001$
P(Colonization)
0.2
0.15
0.1
0.05
0
0
0.5
1
1.5
← Patch Isolation

Figure 6

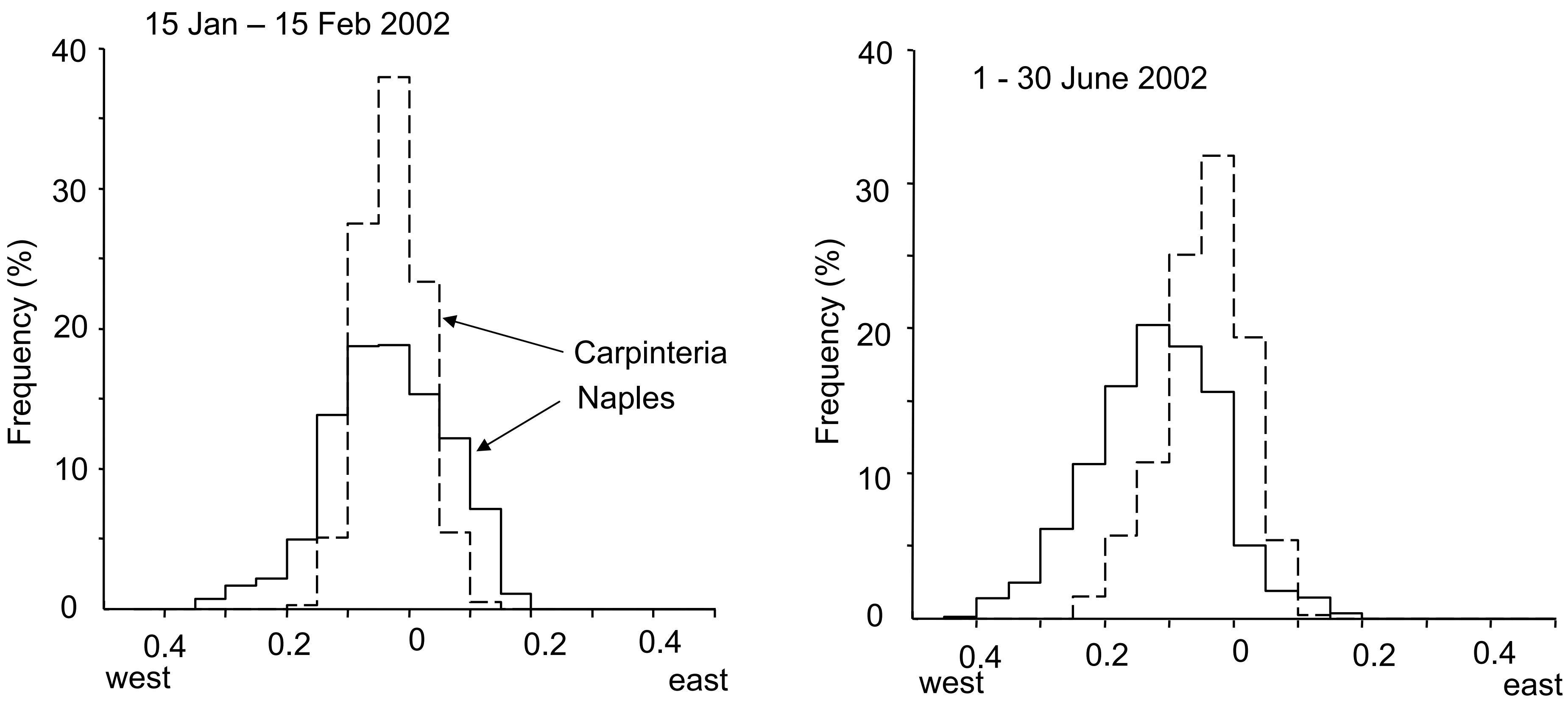


Spores 2.5 mm^{-2} (+/- SE)
40
30
20
10
0
0
10
20
30
40
50
60
Distance from individual plant (m)
100
80
60
40
20
0
0
50
100
150
Distance from edge of kelp bed (m)

Figure 7

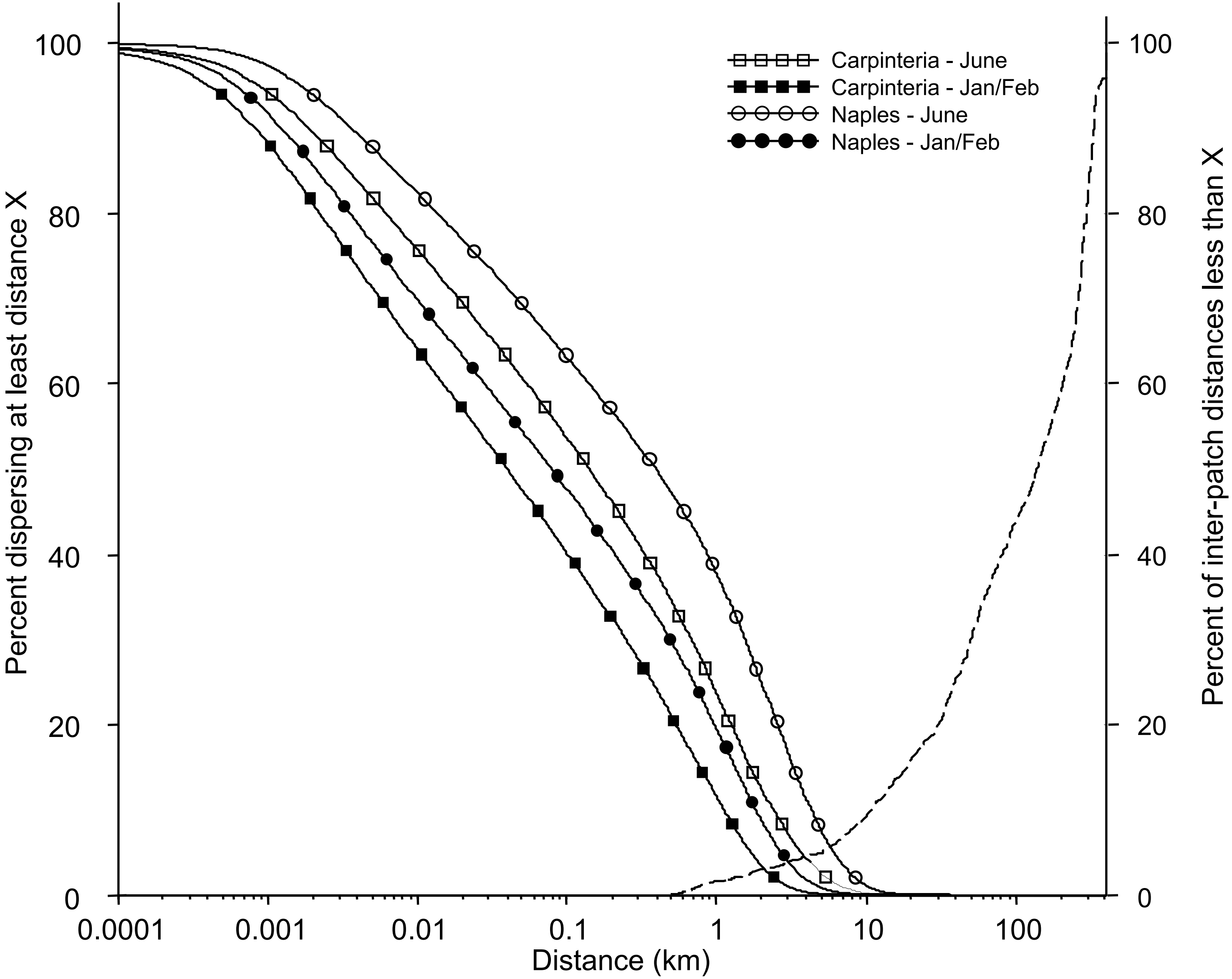


Individual Plants
Kelp bed
Percent of Trials
100
80
60
40
20
0
1
10
100
1000
Estimated Dispersal Distance (m)



Along-shore current speed (m • s^{-1})

Figure 9


Carpinteria - June
Carpinteria - Jan/Feb
Naples - June
Naples - Jan/Feb
Percent dispersing at least distance X
Percent of inter-patch distances less than X
Distance (km)
0.0001
0.001
0.01
0.1
1
10
100
0
20
40
60
80
100
0
20
40
60
80
100

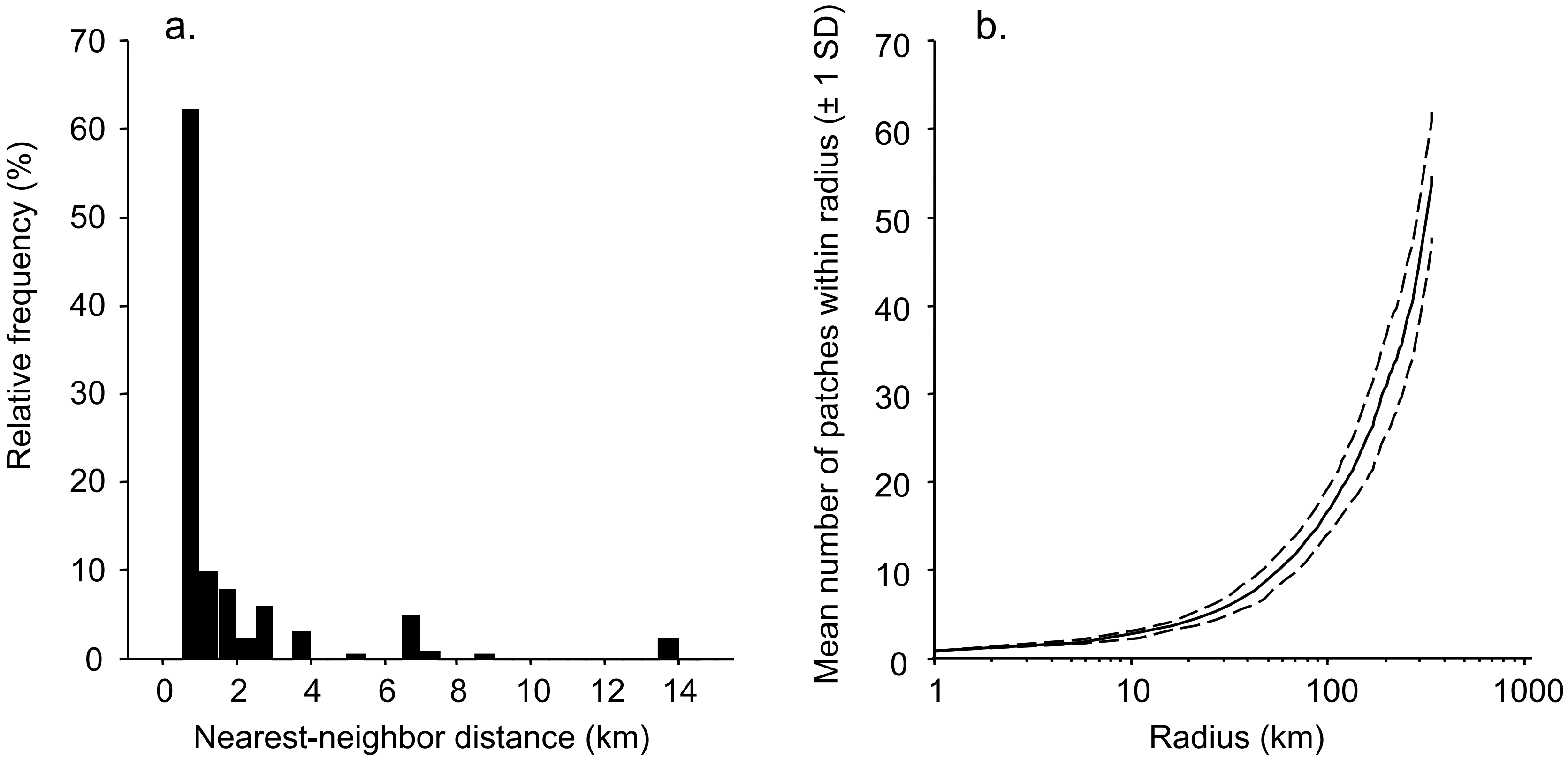
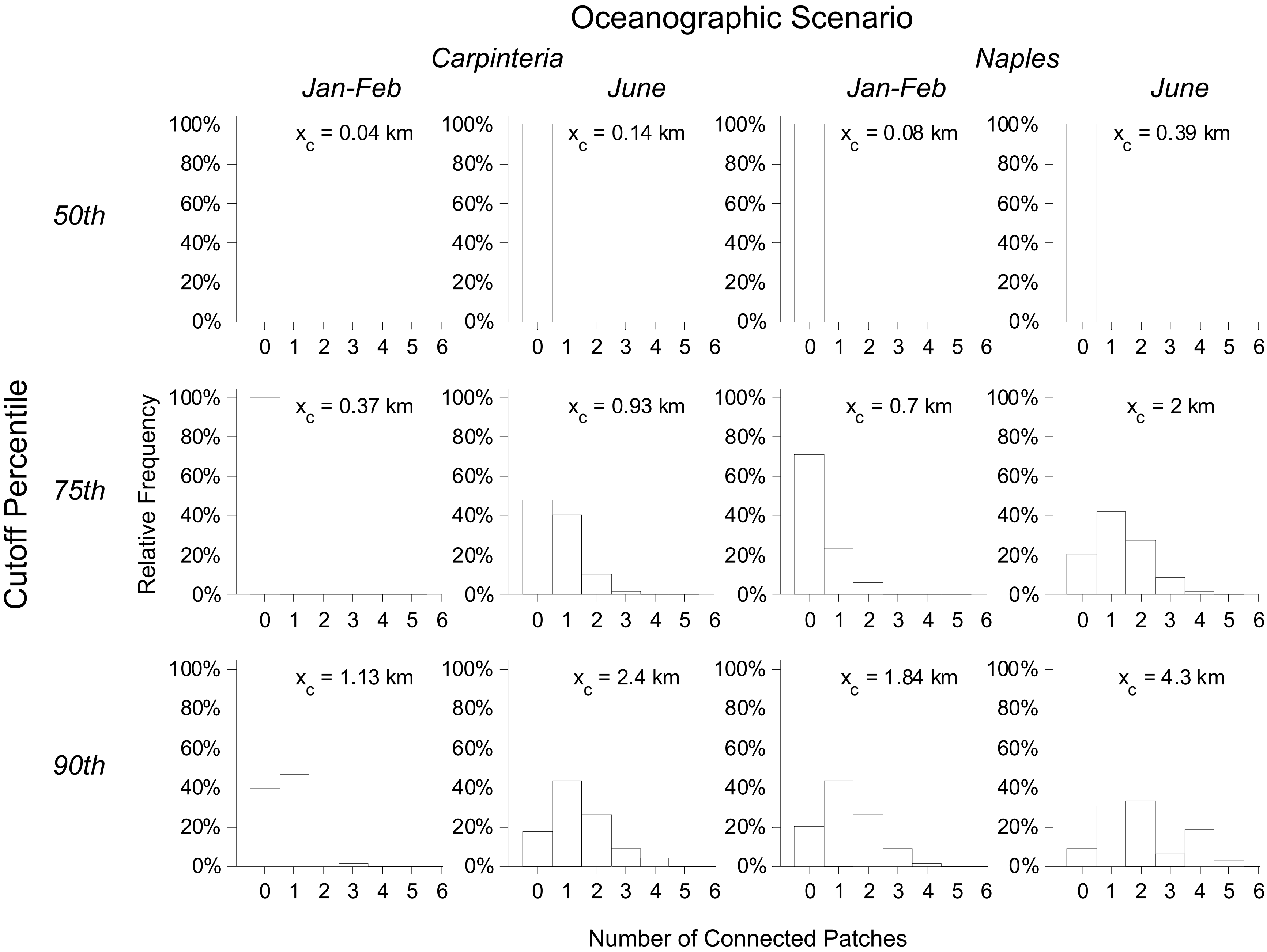

a.
Relative frequency (%)
70
60
50
40
30
20
10
0
0
2
4
6
8
10
12
14
Nearest-neighbor distance (km)
b.
Mean number of patches within radius (± 1 SD)
70
60
50
40
30
20
10
0
1
10
100
1000
Radius (km)

Figure 11


Oceanographic Scenario
Carpinteria
Naples
Jan-Feb
June
Jan-Feb
June
Cutoff Percentile
50th
75th
90th
Relative Frequency
100%
80%
60%
40%
20%
0%
0 1 2 3 4 5 6
x_c = 0.04 km
x_c = 0.14 km
x_c = 0.08 km
x_c = 0.39 km
x_c = 0.37 km
x_c = 0.93 km
x_c = 0.7 km
x_c = 2 km
x_c = 1.13 km
x_c = 2.4 km
x_c = 1.84 km
x_c = 4.3 km
Number of Connected Patches